

THE ALIMENTARY CANAL OF DIPLLOTAXIS LIBERTA GERM. (SCARABAEIDAE: COLEOPTERA)

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This article is a morphological and histological study of the alimentary canal of the scarabaeid beetle *Dipllotaxis liberta* Germ.

The beetle was collected at Westbury, Long Island, New York, while the author was working for the United States Entomological Sub-laboratory. The species is a night flier and about sixty specimens were collected from around street lights and fixed in Kahle's solution, then preserved in seventy-five per cent alcohol. Dr. E. A. Chapin, Taxonomic Investigator, Bureau of Entomology, United States Department of Agriculture, later identified it as *Dipllotaxis liberta* Germ. The beetle is about twelve millimeters long and from reddish brown to black in color. According to Fall (7) it is restricted mainly to the Atlantic Coast States from Massachusetts to Georgia and is occasionally taken west of the Appalachian Mountains.

The author wishes to express his appreciation for the suggestions, criticisms and assistance so freely given by Dr. C. H. Kennedy, and for the helpful comments of many of his fellow students.

GROSS ANATOMY OF THE DIGESTIVE TRACT

General discussion.—The alimentary canal is divided into three main divisions as determined by the embryonic origin. The anterior portion (stomodaeum or fore-intestine) and the posterior portion (proctodaeum and hind-intestine) arise as ectodermal invaginations of the body wall. The epithelium of the mesenteron (ventriculus or mid-intestine) is formed by the proliferation of rings of cells in the endodermal tissue, eventually connecting the fore- and the hind-intestines.

Though there are some variations that occur, the different divisions and sub-divisions will usually be found to lie as follows: the fore-intestine (plate I, fig. 1) passes posteriorly along the median axis to the union of the prothorax and the mesothorax where it joins the mid-intestine. The mid-intestine continues posteriorly along the median axis for about one-third of its length; then it curves to the left and downward, then laterally across the abdominal cavity, making approximately two full spiral curves before looping anteriorly and then posteriorly inside of the second and smaller curve. The union of the mid-

intestine or stomach and the hind-intestine occurs at about the fourth abdominal segment.

The hind-intestine then passes caudally to about the fifth abdominal segment where it enlarges and curves dorsally, then to the right and slightly downward, tapering down to a smaller portion of the alimentary canal. It then curves dorsally and to the left passing over the last curve and a little to the left of the median axis, where it then curves to the right and posteriorly to the anus. The alimentary canal in toto is about thirty-nine and five-tenths millimeters long.

The Fore-Intestine

The fore-intestine is the shortest division of the alimentary canal. It comprises about one-ninth of the total length. The pharynx appears as a short dilated portion posterior to the mouth. The oesophagus connects the pharynx and crop and is a short narrow tube. (See plate I, fig. 1.)

The *crop* (CR) comprises the posterior two-thirds of the fore-intestine. The crop is dilated and is much larger than the oesophagus.

The *oesophageal valve* (OES. V) marks the division of the fore- and mid-intestine by a slight constriction. It is not visible externally.

The Mid-Intestine

The mid-intestine (M. I.) is the largest and longest division of the alimentary canal and comprises about five-ninths of its total length. There are no essential differences in the structures at the two ends, but there is a gradual tapering off in the size from the anterior to the posterior end. The anterior portion is about twice as large in cross-section as the posterior and the size varies with different individuals, depending upon the amount of food present in the canal. Both portions have numerous small crypts upon their outer surfaces.

The Hind-Intestine

The divisions of the hind-intestine are: anterior ileum; posterior ileum; colon; rectum and anus; to the anterior end are attached the malpighian tubules.

The *pyloric valve* (P. V.) forms the junction of the mid-intestine with the hind-intestine and is marked by a slight constriction. The pyloric valve, being internal, is not apparent externally.

The *malpighian tubules* (M. T.) are four in number and are attached separately to the canal, two anterior to the pyloric valve and two posterior to the valve. The two anterior ones are attached on each of the ventro-lateral sides whereas the posterior two empty close together into a bladder on the dorsal side of the anterior end of the ileum. The dorsal tubules are nearly twice as large in diameter as the other two. All are very long, and coiled around close to the canal and extend to the oesophageal valve where they turn posteriorly and terminate with their tips lying upon the mid-intestinal wall.

The *bladder* (BL.) attaches to the dorsal side of the anterior ileum just behind the pyloric valve.

The *anterior ileum* (A. IL.) begins at the division of the mid- and hind-intestine, is the shortest of the four divisions of the intestine, and

tapers off to be the narrowest section of the canal. The caudal or small end of the anterior ileum appears to be constricted at its junction with the posterior ileum but no valve was observed.

The *posterior ileum* (P. IL.) abruptly enlarges following its junction with the anterior ileum; then it tapers off gradually to the size of the colon. Through the thin layers of muscle tissue may be seen numerous folds in the epithelial layer of cells. See plate I, fig. 1, P. IL.

The *colon* (CO.) connects the posterior ileum with the rectum. It is a small uniform tube with well developed muscles on its outer walls. It merges gradually into the *rectum* (REC.) which gradually dilates for a distance, then contracts to the anus. The rectum lies in the region of the sixth, seventh and eighth abdominal segments. As on the colon, the circular and longitudinal muscles are well developed and visible externally.

HISTOLOGICAL STRUCTURE OF THE ALIMENTARY CANAL

The Fore-Intestine.—In general the structure of the fore-intestine is the same throughout though there may be differences in detail.

The innermost layer is the intima, a chitinous layer which is homologous with the cuticula of the body wall. It is continuous throughout the fore-intestine and is a non-cellular homogenous structure. The intima is secreted by the hypodermal epithelial cells and forms a rather thick layer in the mouth (buccal cavity) and pharynx; then it gradually gets thinner as it passes caudally; upon reaching the oesophageal valve it thickens again. In the region of the pharynx it forms spines that protrude inward and caudally but they do not encircle the canal, being found on the folds in the lateral and dorsal sides of the canal. (See fig. 2, plate I.) The intima stains a deep green with Fast Green F. C. F. stain.

The epithelial layer (EPI.) of hypodermal cells just outside of the intima is composed of irregular flattened cells. Their cell walls are apparent but no basement membrane is visible. The cells are of the same character throughout the length of the fore-intestine.

Immediately outside of the epithelium are found the longitudinal muscles (L. M.) which vary in number from isolated strands to layers two or three strands in thickness. In the area of the pharynx and oesophagus they are most numerous and are distributed well around the canal as shown in a cross section. (See fig. 2, plate I.) They gradually become fewer in number towards the crop where only a few isolated strands occur.

The circular muscles (C. M.) lie outside of the longitudinal muscles. Here again, as with the longitudinal muscles, they are the thickest in the region of the oesophagus, being three to four strands thick, gradually diminishing in thickness caudad to one or two thin strands in the region of the crop and then thickening to two or three strands near the oesophageal valve. On the outermost part of the fore-intestine traces of a peritoneal membrane (P. M., fig. 6) composed of connective tissue can be observed here and there, though it is largely obscured by the fatty tissue that surrounds this region of the canal.

The oesophageal valve (fig. 5) which marks the inner division of the junction of the fore- and hind-intestine extends slightly down into the

lumen of the ventriculus as a fold. The valve is composed of an epithelium of hypodermal cells. The cells at the beginning of the fold are of a flattened, irregular type. They soon change to long columnar cells as they extend along the innermost side of the fold; then they gradually decrease in size on the reflexed side; and at the end of the reflexed layer they are cuboidal and join with the cells of the mid-intestine. The intima which continues around the valve disappears at the base of the reflexed layer of cells.

In this region there is a complete reversal of the position of the circular and longitudinal muscles. The circular muscles shift to become the inner layer of muscle fibers on the ventriculus. In the depression formed by the reflexed fold of the valve are numerous circular muscles (C. M.) which serve to close the valve. (fig. 5, plate I.)

Histology of the Mid-Intestine.—A histological study of the mid-intestine shows the following tissues to be much the same in size and structures throughout: (1) epithelium of endoderm cells supported by a basement membrane; (2) circular muscles; (3) longitudinal muscles; (4) "peritoneal" membrane of connective tissue. (fig. 6, plate I.)

The cells of the epithelium vary in shape and size during different periods of the feeding habits of the animal. They may be cuboidal after a period of secretion or they may be columnar during the period of resting, due to the accumulation of the digestive fluids within them. Shortly after feeding, the cells that are filled with the digestive fluid give off the fluid by the cell wall bursting, when the whole, or part, of the contents is expelled into the lumen of the intestine. This is termed the holocrine type of secretion. The burst cells in the holocrine type of secretion are replaced by other cells that are regenerated in the regeneration cell layer at their base or from crypts. These crypts (CRY., fig. 6) are nests of digestive cells which have sunken below both the epithelium and the circular muscles. Within the crypts are developed new cells that replace some of the cells that burst during secretion. The bases of the epithelial cells rest upon a basement membrane. The epithelial layer is generally folded to a greater or lesser degree throughout the length of the canal. Fig. 12 shows the abundance of the crypts as indicated by the distribution of their openings into the stomach.

Immediately outside of the basement membrane lie the circular muscles (C. M., fig. 6) in a layer one strand thick which completely encircle the canal by the interlacing of their ends, when viewed in a cross-section. Still further outward is a single layer of numerous isolated strands of longitudinal muscles. These appear to be connected in places by a thin connective tissue which is probably the peritoneal membrane. The relative position of the longitudinal and circular muscles about the mid-intestine is the reverse of that in the fore- and hind-intestine.

Surrounding the food within the mid-intestine is a very thin structureless peritrophic membrane (PER. M.). It is thought to be secreted by cells at the base of the reflexed layer of cells of the cardiac or oesophageal valve. Its function may be to protect the delicate inner ends of the epithelial cells from the coarse foods.

Histology of the Hind-Intestine.—The origin of the hind-intestine is similar to that of the fore-intestine, being formed from the invagination

of the body wall. The pyloric valve (fig. 7) and the two forward malpighian tubules mark the union of the anterior and with the ventriculus.

A microscopic study of the canal shows the following layers present: (1) an intima; (2) an epithelium of hypodermal cells resting on a basement membrane; (3) longitudinal muscles; (4) circular muscles; (5) "peritoneal" membrane of connective tissue. (figs. 9 and 10, plate II.)

The malpighian tubules (M. T.) are of ectodermal origin, although the two anterior ones appear to open into the ventriculus. They are made up of large irregular cells with oval or spherical nuclei. (figs. 3 and 4, plate I). The number of cells vary from four or five to thirteen or fourteen in a cross-section. The larger sections near the proximal end contain the greater number of cells. The cells secrete fluids by the merocrine type of secretion. Surrounding the mouth of the tubes and extending up in them a short way is a delicate layer of intima, whereas the rest of the inner surface is lined with a striated border. In some sections a striation also appears near the basal side of the cell. The outer surface of the tube is covered with a thin layer of connective tissue.

The pyloric valve (fig. 7) marks the greater part of the internal junction of the mid- and hind-intestine, and consists of a definite folding of the epithelial hypodermal layer into the lumen of the anterior ileum. The cells become extremely elongated and extend out as irregular fan-shaped structures in longitudinal section. The valve consists of two distinct forms of fan-like structure, the central and lateral structure being somewhat flattened and extending downward into the lumen, while the dorsal structure is semicircular with one edge extending into the lumen and the other into the bladder. (fig. 7, plate II.)

The inner surface of the valve is lined with a thin layer of intima, which begins with the cuboidal cells on the anterior side of the valve and extends throughout the ileum in numerous folds. External to the valve and within its folds are a number of circular muscles (C. M., fig. 7) whose function is probably that of closing the valve. A few longitudinal muscles are scattered here and there among them. As at the junction of the fore- and mid-intestine, the muscles here again are reversed in their relative positions.

The bladder (fig. 7) is probably an evagination of the dorsal surface of the ileum, adjacent and caudal to the pyloric valve. The layer of intima lines the inner wall of the bladder. The cells of the epithelium are very irregular, flattened and small. On the outer surface are scattered thin strands of longitudinal and circular muscles. (fig. 7, plate II.)

In the remainder of the ileum (P. IL., fig. 1; and figs. 8 and 11) the layer of epithelium is greatly folded and composed of small irregular shaped cells. Immediately outside of the cell layer are a few isolated strands of longitudinal muscles; outside of these are the circular muscles which vary in thickness from one to two strands in the anterior region and to three or four strands in the posterior region. Outside of the circular muscles are isolated strands of a second layer of longitudinal muscles and a thin layer of peritoneal connective tissue.

The posterior ileum (P. IL., fig. 1) which lies between the anterior ileum and the colon is probably the most outstanding of all the divisions of the canal. The epithelial layer of very irregular cells lies in deep

crosswise folds that are broken by short lengthwise folds; these folds extend into the lumen of the canal, leaving only a small passage for the food throughout the ileum. (See figs. 8 and 11.) These small separate folds are termed by some workers "papillate processes." Surrounding each of them is a thick non-cellular mass of substance that stains a deep green, with Fast Green F. C. F. stain. (fig. 8, plate II, posterior ileum.)

Spines were observed upon the intima at the anterior end of the ileum. The irregularity of the cells probably aids in holding the mass in place. Particles of food sometimes appear between the folds. (fig. 11, plate II, posterior ileum.) Immediately outside of the epithelium is a poorly developed layer of circular muscles. These may be seen at the end of the folds in a cross-section. (fig. 11, plate II, anterior ileum.)

The longitudinal muscles form the outer layer of muscles and are well developed but very thin.

The intima at the anterior end of the ileum is thickened and contains a few spines, while that lining the inner surface of the folds is very delicate and is free of spines.

The ileum gradually merges into the colon. In the colon the intima is of moderate thickness. The circular muscles are the inner layer of muscles. They are well developed and are one to two strands thick. The longitudinal muscle layer is poorly developed and lies as isolated strands and small groups of several strands outside of the circular muscles.

The colon and rectum are very much alike in structure and no difference other than that of size appears. The intima and epithelium are continuous throughout. The epithelium of hypodermal cells that extends throughout the rectum (figs. 9 and 10) is divided into six main longitudinal and several subordinate folds. The outer ends of each of the six main folds are attached to the circular muscles by muscle fiber. The nuclei here, as everywhere else in the canal, are clear and relatively large.

The circular muscles which are in a single layer in the colon gradually become more numerous after they merge with the rectum, until near its center they form a layer four to five strands thick (fig. 10). This then gradually thins down to a layer one strand thick and just anterior to the anus thickens again into a layer nine or ten strands thick. The outer longitudinal muscles are isolated strands. Strands of "peritoneal" membrane of connective tissue appear here and there, all along the outer surface of the hind-intestine. (figs. 9 and 10, plate II.)

SUMMARY

The alimentary canal of *Diplotaxis liberta* Germ. is morphologically divided into three main divisions, namely: fore-intestine, mid-intestine, and hind-intestine. These main divisions are further divided into: Fore-intestine; Pharynx, oesophageal valve. Mid-intestine: entirely stomach. Hind-intestine: Phloric valve, malpighian tubules, bladder, anterior and posterior ileum, colon, and rectum.

The following layers are present: Fore-intestine: Intima, epithelium of hypodermal cells resting on a basement membrane, longitudinal muscles, circular muscles, and "peritoneal" membrane of connective tissue. Mid-intestine: Peritrophic membrane, epithelium of endoderm cells and regenerative cells resting on a basement membrane, circular muscles, longitudinal muscles and "peritoneal" membrane. Hind-intestine: Intima, epithelium of hypodermal cells resting on a basement membrane, inner longitudinal muscles (in anterior end), circular muscles, outer longitudinal muscles and "peritoneal" membrane.

The malpighian tubules are four in number and enter separately into the canal, two anterior to the pyloric valve and two posterior to the valve. The anterior tubules are attached to the ventro-lateral sides and empty directly into the canal; whereas the posterior ones empty into a bladder on the dorsal side which has a common opening into the canal. The bladder is an invagination of the epithelium of the ileum.

The papillate processes of the posterior ileum are folds of the epithelium that project down into the lumen. These folds are covered with a non-cellular mass of material.

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EXPLANATION OF PLATES

PLATE I

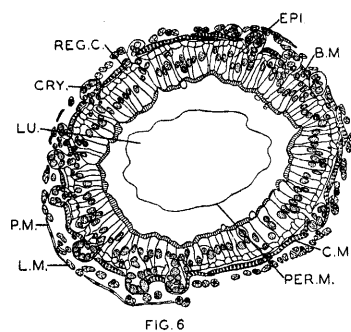
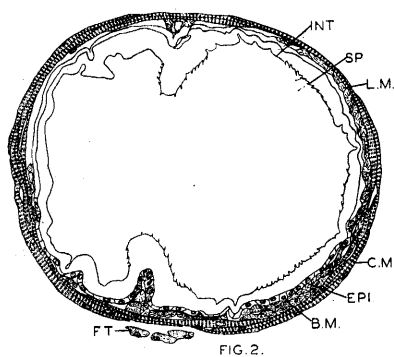
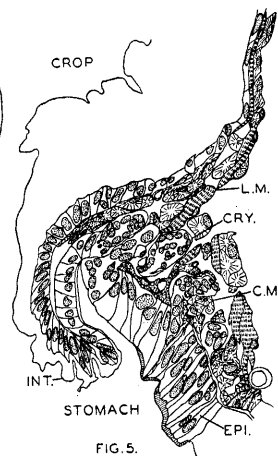
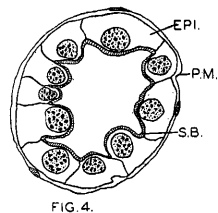
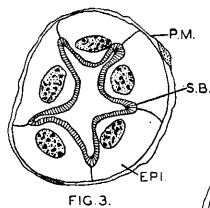
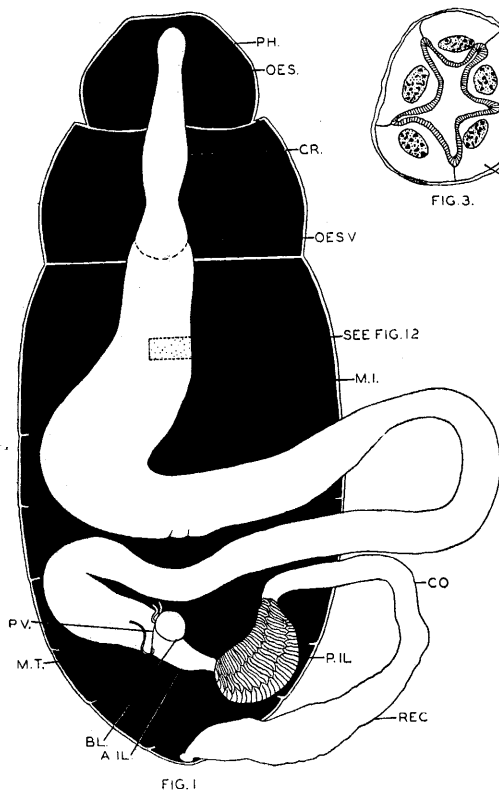
- Fig. 1. Dorsal view showing gross dissection of the alimentary canal of *Diplotaxis liberta* Germ.
 Fig. 2. Cross-section through the oesophagus.
 Fig. 3. Cross-section through malpighian tubule near the distal end.
 Fig. 4. Cross-section through malpighian tubule near the proximal end.
 Fig. 5. Longitudinal section through the oesophageal valve.
 Fig. 6. Cross-section through the mid-intestine.

PLATE II

- Fig. 7. Longitudinal section through the pyloric valve, showing bladder and entrance of malpighian tubule.
 Fig. 8. Cross-section through the posterior ileum.
 Fig. 9. Cross-section through the rectum near the anterior end, showing the relationship of the muscles.
 Fig. 10. Cross-section through the rectum near the middle.
 Fig. 11. Portion of a cross-section of the posterior ileum enlarged, showing the papillate processes.
 Fig. 12. Diagram of a portion of the external wall of the mid-intestine greatly enlarged, showing the number of crypts per unit area.

KEY TO ABBREVIATIONS

A. IL.	Anterior Ileum	M. T.	Malpighian tubule
BL.	Bladder	OES.	Oesophagus
B. M.	Basement Membrane	OES. V. . . .	Oesophageal Valve
C. M.	Circular Muscles	PA. PR. . . .	Papillate process
CO.	Colon	PER. M. . . .	Peritrophic membrane
CR.	Crop	HP.	Pharynx
CRY.	Crypt	P. IL.	Posterior ileum
EPI.	Epithelium	P. M.	Peritoneal membrane
FD.	Food	P. V.	Pyloric Valve
F. T.	Fat tissue	REC.	Rectum
INT.	Intima	REG. C. . . .	Regenerative cell
L. M.	Longitudinal Muscle	S. B.	Striated Border
LU.	Lumen	SP.	Spines
M. I.	Mid-intestine		



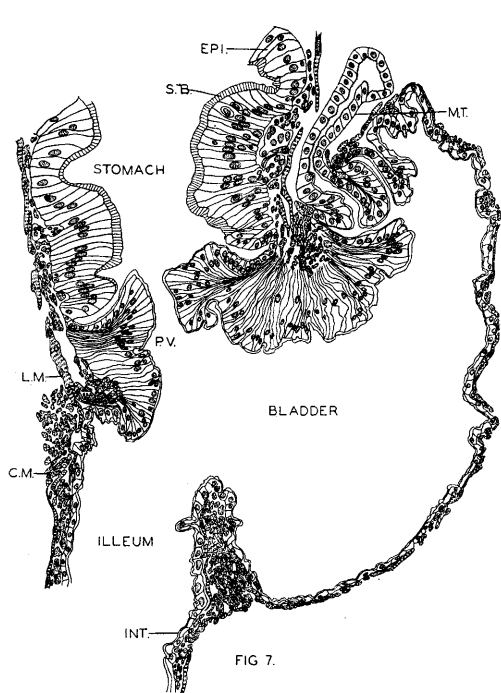


FIG. 7.

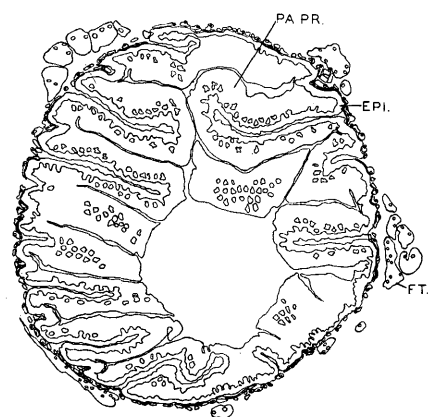


FIG. 8.

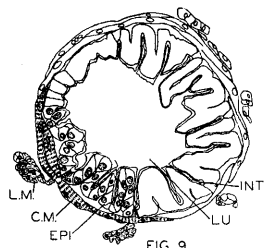


FIG. 9.

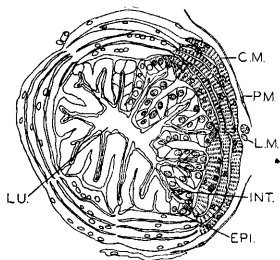


FIG. 10.

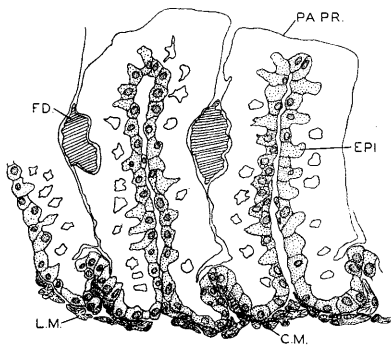


FIG. 11.

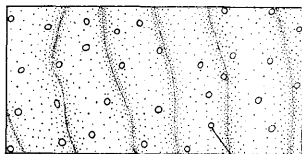


FIG. 12.